Article

Conspicuousness and toxicity of Coccinellidae: An aposematic review

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Abstract
Coccinellids (commonly known as ladybirds) mostly exhibit bright clouration and play a vital role in biological control of pests of important crops such as aphids and scale insects. Nevertheless, they are characterized by the possession of a group of unpleasant and poisonous defence chemicals. These chemicals along with bright colouration form an aposematic enemy barrier. Many conspicuously coloured adults of coccinellidae have elytra with contrasting red-and-black or yellow-and-black patterns generally serving as aposematic (warning) colouration. Larvae and pupae of ladybirds may also be aposematically coloured with dark and bright areas on their surface. In this review, the significance of colouration and toxicity in ladybirds has been highlighted.

Keywords aposematism; warning signals; chemical defence; carotenoids; alkaloids.

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1 Introduction

1.1 Aposematism

Many animals discourage predators through advertisement (warning signals) about their toxicity, unpalatability or otherwise unsuitability as prey items. This is known as aposematism and is usually beneficial to both predators and prey as predators evade the costs of utilizing inappropriate food (including wastage of energy to sickness or even death) and the prey eludes from the predator's attack. Most animals possess bright colours to warn predators of their defences, nonetheless, it is uncertain whether the levels of defence are reliably designated by the strength of warning colours. Two constituents of aposematism include: a primary defence like characteristic colour or smell which indicates the unsuitability of the prey and thus helps to avoid attack; and a secondary defence that includes chemical toxicity and is exercised by the prey when attacked by the predator. For example, the bright colouration (red, orange or yellow) of the wings of ladybirds along with black spots is an advertisement to the predators that they are toxic (Arenas et al., 2015).

Wallace (1889) originally put forward the concept of warning signals for the brightly coloured caterpillars which were apparently incongruous with the theory of natural selection at that time (Winters, 2018). Wallace mentioned the expression of poisonous features as “warning colouration” and the early studies of brightly coloured aposematic signals were mostly limited to the visual perspective only. Now, conspicuous colouration, sounds, odours or other perceivable characteristics have been included among the aposematic signals (Rowe and Guilford 1999). “Aposematism” is a Greek word used for the first time by Poulton (1890) to depict the Wallace’s perception of warning colouration.

1.2 Evolution of aposematism

From the evolutionary perspective, aposematism seems to be paradoxical because aposematic displays make the bearers noticeable to the predators, as a result of which they may be eliminated by killing and the trait can be lost before the predator’s learning to avoid it (Briolat et al., 2019). Although the advertisement of unpalatability is clearly beneficial to predators and many species are characterized by aposematic displays, the origin of aposematic traits is less straight. Darwin (1874) speculated that sexual selection is responsible for the origin of bright plumage and other conspicuous traits and these are used primarily by the males to attract females.

The efficacy of aposematic displays increases with their density/frequency. Multiple theories have been suggested to explain the survival of first individuals with mutations that strengthen conspicuousness to assist predator learning and consequently accomplish a selective advantage (Skelhorn et al., 2016). Amongst these, some are concerned with the stochastic situations like the absence of predators temporarily, survival of the mutants by chance or arbitrary shifts in prey population dynamics (Winters, 2018) while others hypothesize non-mutation based origin of aposematism (Ruxton et al., 2004). Aposematic signals might evolve due to their role in other activities like mating (i.e. sexual selection), searching for food, or temperature regulation with the continuation of evolutionary process including multiple selective pressures. Likewise, unperturbed selection on crypsis may contribute to the evolution of aposematic signals in case of dense population of the prey and high possibility of finding by the predators. An abrupt environmental change that initiates a previously cryptic signal to modify into a conspicuous one may also be the cause of aposematism.

The above mentioned hypotheses are, however, not mutually exclusive and the evolution of aposematism occurred through different routes in different species with the passage of time. Advances in the study of evolutionary processes such as phylogenetic analyses and reconstructions may be helpful in understanding the origin of aposematic organisms (Härlin and Härlin, 2003).

1.3 Characteristics of aposematic display

Generally, an effective warning display is one that facilitates long-term learning and avoidance by the predator. In spite of the diversity of aposematic displays, most of them also have several common features, which are associated with their functions. Usually, the aposematic displays exhibit conspicuousness including elements like bright colouration or powerful odours. Several reasons have been listed to explain the suitability of conspicuous colours to an aposematic display (Stevens and Ruxton, 2011).

Due to conspicuousness, detection and species identity becomes easy for the predator at a distance. Conspicuous aposematic displays may add to the predator vigilance and increase predator learning, remembering and prey identification precision as compared to other types of signals.

Apart from general conspicuousness, aposematic displays are mostly characterized by other related features (Stevens and Ruxton, 2011). Aposematic warning signals mostly comprise similar colours, usually red, yellow, and black. The reason for this may be that the usage of similar colours enables the aposematic species to minimize species-level learning costs when the avoidance of these aposematic colours is learnt by the predators either individually or through evolutionary time. Many aposematic species share same phenotype to get benefit in Müllerian mimicry. Nevertheless, the common use of red, yellow and black is important with respect to the environment. In comparison to other colours, these colours have a strong contrast with green foliage background, persist distinct in shadow and lighting, show distinctiveness in both colouration as well as brightness and exhibit distance dependent camouflage (Stevens and Ruxton, 2011).

Regardless of the above-mentioned general features, aposematic displays show variations both within species and among closely associated species. Environmental variation or predator community, with respect to seasons or space, are important to maintain this diversity which may be helpful for different morphs to flourish in different times, areas or contexts. There might be involvement of further selective pressures with phenotypes showing an association between aposematism and other phenomena such as sexual selection.

1.4 Signal honesty

Honest signalling has been described in association with handicap hypothesis, which suggests that displays are honest because high costs are related to their production (Penn and Számadó, 2019). However, aposematic displays are not essentially handicaps and there is no consistent link between the mechanisms of aposematic display production and secondary defences (Guilford and Dawkins, 1993). Qualitatively, prey unpalatability is often honestly revealed by the conspicuous aposematic displays as prey lacking secondary defences, such as toxicity, is incapable to disburse for the survival costs of being more prominent to predators (Summers et al., 2015). In absence of secondary defence, conspicuous aposematic displays will result in high rates of predation and reduced fitness. Batesian mimicry is the major exception whereby an undefended species mimics an aposematic species for the sake of getting fitness advantages of the aposematic one without experiencing the costs of defence.

Exhibition of quantitative honest displays by some aposematic species indicates that the strength of aposematic display positively correlates to the degree of predator’s unpalatability (Summers et al., 2015). Qualitative honesty seems to be more common than this, though it needs further research. Quantitatively honest aposematic displays may be predominantly liable when there is morphological or physiological relation of the signal to the mode of defence (Winters, 2018).

2 Aposematism in Coccinellidae

Ladybirds (Coleoptera: Coccinellidae) are famous for their bright colouration and for their important role in the biological control of pests of valuable crops like aphids and scale insects. Nevertheless, they possess unpleasant and toxic defensive chemicals which along with bright colouration make ladybirds truly aposematic (Ceryngier et al., 2012). Especially the best known tribe Coccinellini is characterized by colourful adults with contrasting patterns of red-and-black or yellow-and-black on their elytra serving as aposematic (warning) colouration (Escalona et al., 2017). The body surface of larvae and pupae also consists of aposematically coloured dark and bright areas (Holloway et al., 1991). For some optically oriented vertebrate predators like the great tit (*Parus major*), any spotted pattern and general body shape (oval and convex) may also serve as signal of prey unprofitability besides warning colouration (Dolenská et al., 2009).

A wide range of variation in colouration is common not only among the members of Coccinellidae family but also within some peculiar species exhibiting several colour forms (e.g. *Adalia bipunctata* and *Adalia decempunctata*: Honěk et al., 2005; *Harmonia axyridis*: Kholin, 1990). There is a distinct variation in the number and size of the spots. Plain colouration is characteristic for smaller species such as black Scymnini, unspotted reddish *Coccidula rufa* and brownish *Cynegetis impunctata* (Majerus, 1994).

2.1 Pigments in ladybirds

Carotenoid pigments are found in many insects (Goodwin, 1971), for example, beetles, including orange-red colour of the ladybird beetles. Generally, *de novo* synthesis of carotenoids has never been reported in animals including insects, consequently, those found in animals are of dietary origin (Goodwin, 1952). Metabolic reactions can be responsible for their partial modification (Liaaen-Jensen, 1990; Matsuno, 1989). The carotenoids identified in *Coccinella septempunctata* are probably of microbial, not plant, origin indicating the contribution of symbiotic microorganisms (Britton et al., 1977).

2.2 Toxicity of Coccinellidae

Ladybirds are chemically defended against predators by the possession of unpleasant and toxic chemical compounds present in their haemolymph, the most common of which are alkaloids, polyazamacrolides, and polyamines (Laurent et al., 2005). In addition to these compounds, haemolymph of ladybirds also contains chemicals known as pyrazines, which provide olfactory long-distance anti-predatory protection (Guilford et al., 1987; Rothschild and Moore, 1987). Olfactory orienting predators like ants (Sloggett et al., 1998), spiders (Camarano et al., 2006), lacewings (Lucas, 2005), and other ladybirds (Agarwala and Dixon, 1992) avoid to attack ladybirds due to their chemical signals. Some ladybird species are found very toxic to birds (Marples, 1993; Marples et al., 1989). The ladybird haemolymph contains the following major toxic elements:

2.3 Alkaloids

Many ladybirds produce alkaloids which are basic, nitrogen-containing natural compounds and have bitter taste and toxic properties (Daloze et al., 1995). Nearly 50 different types of alkaloids have been studied in ladybirds (Laurent et al., 2005) which are manufactured in their haemolymph including acyclic amines, pyrrolidines, piperidines, 9-azabicyclononanes (homotropanes), 2-methylperhydro-9b-azaphenalenes and azamacrolides. On disturbance, ladybirds emit droplets of their haemolymph at their tibio-femoral joints, which is known as ‘reflex blood’ and this emission is called ‘reflex bleeding’. This mechanism is an efficient defence against predators due to the presence of distasteful and toxic alkaloids (Daloze et al., 1995). Reflex bleeding is common in adults of most ladybird species while in some species, larvae and/or pupae also reflex bleed through the pores of the dorsal surface of the body (Holloway et al., 1991).

The correlation of the existence of alkaloids with the aposematic colours and not with being phytophagous or carnivorous has been established from a survey of 30 different ladybird species (Braekman et al., 1998). Several studies have shown the deterrence activity of the bitter-tasting alkaloids of ladybirds towards ants (Pasteels et al., 1973; Aslam and Nedvěd, unpublished) and jumping spiders (Eisner et al., 1986). Although the toxic effects of ladybirds to nestlings of birds are relatively variable, *Coccinella septempunctata* has been found to be highly toxic to nestling blue tits (Marples et al., 1989).

2.4 Pyrazines

The idea of “olfactory aposematism” proposed by Eisner and Grant (1980) reveal an association of odours and toxicity and resulting avoidance to attack toxic or unpalatable organisms based on their smell. Chemically, 2-methoxy-3-alkylpyrazines found in the haemolymph of ladybirds are aromatic heterocyclic nitrogen containing compounds. When these insects reflex bleed, pyrazines produce the typical odour which, together with aposematic colouration, warns the predators of the unpalatability of ladybirds (Moore et al., 1990).

2.5 Polyamines

Polyamines are organic compounds comprising more than two amino groups. Mixture of macrocyclic polyamines constitutes the major portion of the pupal defensive secretion of phytophagous ladybird *Epilachna borealis*. These compounds include very large-ring lactonic structures derivative of 2-hydroxyethylamino alkanoic acids. A high structural diversity is generated by the combinatorial assembly of the small building blocks with an additional intramolecular reorganisation of the macrocycles (Schröder et al., 1998).

3 Relationship Between Conspicuousness and Toxicity

The signalling role of carotenoids and melanin-based colours in invertebrates is not well investigated. *Harmonia axyridis* may be a model organism for such type of studies due to the great variation of red and black patches on the elytra and the chemical defence with an alkaloid, harmonine. It has been revealed that the visual signal strength is positively correlated with the level of toxicity in the harlequin ladybird *H. axyridis* (Bezzerides et al., 2007). Similar results have been found in the conspicuously coloured poison frog family (Dendrobatidae) (Summers and Clough, 2001). *Harmonia axyridis* females were particularly found having more red (or less black) elytra with high alkaloid content as compared to males, and non-melanics have better chemical defence (Bezzerides et al., 2007). In a supportive argument for this, use of antioxidant molecules for both pigmentation and protection against accumulated toxins has been proposed; hence, conspicuousness and toxicity may be described to be positively correlated due to the presence of these molecules (Blount et al., 2009).

In conclusion it is argued that conspicuousness and toxicity should be correlated, however, the study of Aslam (2020) revealed that repellency and toxicity of cryptic and less aposematic ladybird species were not systematically lower than those of conspicuous species.

References

Agarwala BK, Dixon AFG. 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. Ecological Entomology, 17: 303-309

Arenas LM, Walter D, Stevens M. 2015. Signal honesty and predation risk among a closely related group of aposematic species. Scientific Reports, 5: 11021

Aslam M. 2020. Aposematism and Toxicity of Coccinellidae. Ph.D. Thesis Series No. 5. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic

Bezzerides AL, McGraw KJ, Parker RS, Husseini J. 2007. Elytra colour as a signal of chemical defence in the Asian ladybird beetle *Harmonia axyridis*. Behavioural Ecology and Sociobiology, 61: 1401-1408

Blount JD, Speed MP, Ruxton GD, Stephens PA. 2009. Warning displays may function as honest signals of toxicity. Proceedings of the Royal Society of London B, 276:871-877

Braekman JC, Daloz D, Pasteels JM. 1998. Alkaloids: Biochemistry, Ecology and Medicinal Applications. Ed: Roberts and Wink. Plenum Press, New York, USA

Briolat ES, Burdfield ‐ Steel ER, Paul SC, Rönkä KH, Seymoure BM, Stankowich T, Stuckert AM. 2019. Diversity in warning colouration: selective paradox or the norm? Biological Reviews, 94(2): 388-414

Britton G, Lockley WJ, Harriman GA, Goodwin TW. 1977. Pigmentation of the ladybird beetle *Coccinella septempunctata* by carotenoids not of plant origin. Nature, 266(5597): 49

Camarano S, Gonzalez A, Rossini C. 2006. Chemical defence of the ladybird beetle *Epilachna paenulata*. Chemoecology, 16: 179-184

Ceryngier P, Roy EH, Poland RL. 2012. Natural enemies of ladybird beetles. In: Ecology and Behaviour of the Ladybird Beetles (Coccinellidae). Blackwell Publishing Ltd, USA

Daloze D, Braekman JC, Pasteels JM. 1995. Ladybird defence alkaloids: structural, chemotaxonomic and biosynthetic aspects (Col.: Coccinellidae). Chemoecology, 5(3-4): 173-183

Darwin C. 1874. The descent of man and selection in relation to sex. John Murray, London, UK

Dolenska M, Nedved O, Vesely P, Tesarova M, Fuchs R. 2009. What constitutes optical warning signals of ladybirds (Coleoptera: Coccinellidae) towards bird predators: colour, pattern or general look? Biological Journal of the Linnean Society, 98: 234-242

Eisner T, Grant RP. 1980. Toxicity, odor aversion, and ‘‘olfactory aposematism’’. Science, 213: 476

Eisner T, Goetz M, Aneshansley D, Ferstandig-Arnold G, Meinwald J. 1986. Defensive alkaloid in blood of Mexican bean beetle (*Epilachna varivestis*). Experientia, 42(2): 204-207

Escalona HE, Zwick A, Li HS, Li J, Wang X, Pang H, Hartley D, Jermiin LS, Nedvěd O, Misof B, Niehuis O. 2017. Molecular phylogeny reveals food plasticity in the evolution of true ladybird beetles (Coleoptera: Coccinellidae: Coccinellini). BMC Evolutionary Biology, 17(1): 151

Goodwin TW. 1952. The Comparative Biochemistry of the Carotenoids. Chapman and Hall, London, UK

Goodwin TW. 1971. Chemical Zoology VI, Arthropoda B (Florkin M, Scheer BT, eds). 290-306, Academic Press, New York, USA

Guilford TIM, Nicol C, Rothschild M, Moore BP. 1987. The biological roles of pyrazines: evidence for a warning odour function. Biological Journal of the Linnean Society, 31(2): 113-128

Guilford T, Dawkins MS. 1993. Are warning colours handicaps? Evolution, 47: 400-416

Härlin C, Härlin M. 2003. Towards a historization of aposematism. Evolutionary Ecology, 17: 197-212

Holloway GJ, de Jong PW, Brakefield PM, de Vos H. 1991. Chemical defence in ladybird beetles (Coccinellidae). I. Distribution of coccinelline and individual variation in defence in 7-spot ladybirds (*Coccinella septempunctata*). Chemoecology, 2(1): 7-14

Honěk A, Martínková Z, Pekar S. 2005. Temporal stability of morph frequency in central European populations of *Adalia bipunctata* and *A. decempunctata* (Coleoptera: Coccinellidae). European Journal of Entomology, 102: 437-442

Kholin SK. 1990. Stability of the genetic-polymorphism in colour of *Harmonia axyridis* Pall. (Coccinellidae, Coleoptera) in maritime province, USSR. Genetika, 26: 2207-2214

Laurent P, Braekman JC, Daloze S. 2005. Insect chemical defence. Chemistry of Pheromones and other Semiochemicals , II: 167-229

Liaaen-Jensen S. 1990. Marine carotenoids-selected topics. New Journal of Chemistry, 14: 747-759

Lucas E. 2005. Intraguild predation among aphidophagous predators. European Journal of Entomology, 102: 351–363

Majerus MEN. 1994. Ladybird. Harper Collins. London, UK

Marples N. 1993. Toxicity assays of ladybirds using natural predators. Chemoecology, 4: 33-38

Marples NM, Brakefield PM, Cowie RJ. 1989. Differences between the 7-spot and 2-spot ladybird beetles (Coccinellidae) in their toxic effects on a bird predator. Ecological Entomology, 14: 79-84

Matsuno T. 1989. Marine carotenoids. Marine Biogenic Lipids, Fats, and Oils, 1: 251-388

Moore BL, Brown WV, Rothschild M. 1990. Methylalkylpyrazines in aposematic insects, their hostplants and mimics. Chemoecology, 1: 43-51

Pasteels JM, Deroe C, Tursch B, Braekman JC, Daloze D, Hootele C.1973. Distribution et activites des alcaloides defensifs des Coccinellidae. Journal of Insect Physiology, 19(9): 1771-1784

Penn DJ, Számadó S. 2019. The Handicap Principle: how an erroneous hypothesis became a scientific principle. Biological Reviews, 204849107

Poulton EB. 1890. The Colours of Animals: Their Meaning and Use, Especially Considered in The Case Of Insects. D. Appleton and Company, New York, USA

Rothschild M, Moore B. 1987. Pyrazines as alerting signals in toxic plants and insects. In: Insects-Plants (Labeyrie V, Fabres G, Lachaise D, eds). 97-101, Dr W. Junk, Dordrecht, Netherlands

Rowe C, Guilford T. 1999. The evolution of multimodal warning displays. Evolutionary Ecology, 13: 655-671

Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry. Oxford University Press, New York, USA

Schröder FC, Farmer JJ, Attygalle AB, Smedley SR, Eisner T, Meinwald J. 1998. Combinatorial chemistry in insects: a library of defensive macrocyclic polyamines. Science, 281(5375): 428-431

Skelhorn J, Halpin CG, Rowe C. 2016. Learning about aposematic prey. Behavioral Ecology, 27: 955-964

Sloggett JJ, Wood RA, Majerus MEN. 1998. Adaptations of *Coccinella magnifica* Redtenbacher, a myrmecophilous coccinellid, to aggression by wood ants (*Formica rufa* group). I. Adult behavioral adaptation, its ecological context and evolution. Journal of Insect Behavior, 11: 889-904

Stevens M, Ruxton GD. 2011. Linking the evolution and form of warning colouration in nature. Proceedings of the Royal Society B: Biological Sciences, 279(1728): 417-426

Summers K, Clough ME. 2001. The evolution of colouration and toxicity in the poison frog family (Dendrobatidae). Proceedings of the National Academy of Sciences of USA, 98: 6227-6232

Summers K, Speed MP, Blount JD, Stuckert AMM. 2015. Are aposematic signals honest? A review. Journal of Evolutionary Biology, 28: 1583-1599

Wallace AR. 1889. Darwinism: An exposition of The Theory of Natural Selection with Some of Its Applications. Macmillan and Co. London, UK

Winters S. 2018. Aposematism. In: Encyclopedia of Animal Cognition and Behavior (Vonk J, Shackelford T, eds). Springer, Netherlands